

**Acanthocephala including the descriptions of new species of *Centrorhynchus* (Centrorhynchidae) and the redescription of *Lueheia inscripta* (Westrumb, 1821) (Plagiorhynchidae) from birds from Paraguay South America**

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**Acanthocephala including descriptions of new species of *Centrorhynchus* (Centrorhynchidae) and the redescription of *Lueheia inscripta* (Westrumb, 1821) (Plagiorhynchidae) from birds from Paraguay South America.** - Acanthocephalans from bird hosts that could not be identified are listed. Centrorhynchidae, including *Centrorhynchus guira* Lunaschi & Drago, 2010 and four new species *C. geranoaeti*, *C. millerae*, *C. pitangi* and *C. viarius* are reported from Paraguay for the first time. Two additional new species, centrorhynchids, were identified but could not be described fully because of insufficient material. The new species are distinguished from congeners principally by the characters of the proboscis armature and further by a combination of the morphometrics of the organs in the trunk, including the male reproductive system, and the size of the eggs. *Lueheia inscripta* (Westrumb, 1821) is reported from Paraguay for the first time and redescribed. The taxonomic position of *C. opimus* is confirmed, *Centrorhynchus polymorphus* is considered a junior synonym of *Sphaerirostris polymorphus* and *Lueheia karachiensis* declared *incertae sedis*.

**Keywords:** Parasite - Acanthocephala - *Centrorhynchus* - *Lueheia* - South America - Paraguay - birds.

## INTRODUCTION

The Acanthocephala from South American birds have not been extensively studied and there has been only a single report, *Centrorhynchus albidus* Meyer, 1933 from a falcon, from Paraguay (Golvan, 1956). An analysis of the family Centrorhynchidae has shown that 10 other species of *Centrorhynchus*, namely *C. croto-phagicola* Schmidt & Neiland, 1966, *C. giganteus* Travassos, 1921, *C. guira* Lunaschi & Drago, 2010, *C. kuntzi* Schmidt & Neiland, 1966, *C. microcephalus* (Bravo-Hollis, 1947), *C. nicaraguensis* Schmidt & Neiland, 1966, *C. opimus* (Travassos, 1921), *C. polymorphus* Travassos, 1926, *C. simplex* Meyer, 1932 and *C. tumidulus* (Rudolphi, 1819) are known from Central and South America; Argentina, Brazil, Mexico, Nicaragua, Panama, Paraguay, Puerto Rico, Uruguay and Venezuela (Petroschenko, 1958; Whittaker *et al.*, 1970a; Vicente *et al.*, 1983; Vizcaino, 1993; Golvan, 1994;

Lunaschi & Drago, 2010). Reassigned from *Centrorhynchus* to *Sphaerirostris* by Golvan (1956, 1960) and then returned to *Centrorhynchus* by Golvan (1994), the status of *C. opimus* is discussed below. The position of *C. polymorphus* also needs consideration. Both Dimitrova & Gibson (2005) and Lunaschi & Drago (2010) have suggested that it might better fit the genus *Sphaerirostris* than the genus *Centrorhynchus*.

Two genera of the Plagiorhynchidae, *Plagiorhynchus* and *Lueheia* are found in South American birds but there have been no previous reports of plagiorhynchids from Paraguay. Four species of *Plagiorhynchus* have been described from Brazil (Travassos, 1926) but not reported on since. Two species of *Lueheia*, *L. lueheia* Travassos, 1921 and *L. inscripta* (Westrumb, 1821), were originally described from Brazil (Travassos, 1921, 1926). *Lueheia inscripta* was subsequently reported from Mexico, Nicaragua, Panama and Puerto Rico (Schmidt & Neiland, 1966; Acholonu, 1976; Whittaker *et al.*, 1970b; Golvan, 1994; Calegaro-Marques & Amato, 2010; Salgado-Maldonado & Caspeta-Mandujano, 2010) and a third species, *L. cajabambensis* Machado-Filho & Nicanor-Ibáñez, 1967 was reported from Peru (Machado-Filho & Nicanor-Ibáñez, 1967; Tantaleán *et al.*, 2005). A fourth species, *L. adluheia* (Werby, 1938) has been described from the United States of America (Werby, 1938) and accepted as valid by Van Cleave & Williams (1951), Amin (1985), Golvan (1994), Aly Khan *et al.* (2005) and Salgado-Maldonado & Caspeta-Mandujano (2010) but placed as a synonym of *L. inscripta* by Van Cleave (1942), Yamaguti (1963), Schmidt & Neiland (1966) and Schmidt & Kuntz (1967). Each of the above species occurs in passerine bird hosts. Recently a fifth species, *L. karachiensis* Aly Khan, Bilqees & Muti-ur-Rehman, 2005, has been described from a raptor, *Accipiter badius cenchroides* (Seretzov, 1873) from India. The validity or otherwise of these latter two species needs further consideration given the lack of agreement by various authors with regard to *L. adluheia* and that *L. karachiensis* is geographically isolated from other species of *Lueheia* and not found in a passerine host.

Between 1982 and 1989 the Muséum d'Histoire Naturelle, Geneva (MHNG) sponsored a series of surveys of the vertebrate fauna of Paraguay. As part of this programme acanthocephalans were collected from eight orders of birds comprising 46 species from 11 families. In this paper acanthocephalans from the families Centrorhynchidae and Plagiorhynchidae are documented, new host and geographic records are reported, new species of *Centrorhynchus* are described and the systematic position of *C. opimus* and *C. polymorphus* and the validity of *L. adluheia* and *L. karachiensis* are discussed.

## MATERIALS AND METHODS

The birds examined included 36 individuals of 26 species from 17 families from which plagiorhynchids, centrorhynchids and specimens that could not be fully identified were dissected. The collection localities of the hosts, with the number of hosts in parentheses, were as follows:

Alto Paraguay Department General Diaz (1). – Alto Parana Department Itaipu (1). – Boqueron Department Pratt's Gill (1); Pedro P Pena (1); Route Montani –Madrigon 2 (1). – Concepcion Department Aquidaban (1); Santa Sofia 10E (1);

Arroyo Tagatiya-Guazu (1); Puente Zinho (1); Arroyo Tagatija-Mi (1). – Cordillera Department Rio Piribebuy (1); Tobati (1). – Itapua Department Arroyo Agua-Pey (4); Santa Maria (1). – Central Department S-Lorenzo N 10e (6). – Paraguari Department 15 Km E From Cerrito (1). – Presidente Hayes Department Transchaco 70 (1); Transchaco 110 (1); Transchaco 115 (1); Transchaco 180 (1); Transchaco 293 (3); Puerto Militar 35 (1); Pozo Arias (1). – San Pedro Department Arroyo Tapiracuai (1); Rio Guazu, Rte 3, Jejui (2).

On dissection all specimens were fixed with neutral buffered 4% formalin and stored in 75% ethanol. Before microscopic examination all specimens were cleared in lactophenol or beechwood creosote to be studied as wet mounts. All measurements made using an eyepiece micrometer are given in micrometres, unless otherwise stated, with the range followed by the mean in parentheses. Measurements of the neck were taken from the base of the proboscis to the level just anterior to the insertion of the lemnisci and measurements of proboscis width at the widest part anterior to the insertion of the proboscis receptacle. Illustrations were made with the aid of a drawing tube.

The terminology for describing proboscis hook types follows Lunaschi & Drago (2010): that is – true hooks with roots with or without manubria, transitional hooks with manubria and without roots and spiniform hooks without manubria or roots. Where the presence or absence of transitional hooks is not noted in the description all hooks other than true hooks are counted as spiniform hooks, following Schmidt & Neiland (1966). All specimens collected for this study are registered in the MHNG.

## RESULTS

Of the acanthocephalans centrorthynchids, all *Centrorthynchus* spp., were found in 16 hosts and a plagiorthynchid, *Lueheia inscripta*, in 5 hosts (Table 1). A further 9 hosts were infected with adult acanthocephalans, specimens that had damaged, missing or inverted proboscides and could not therefore be identified further. Six hosts were infected with cystacanths, some of which could be identified as *Centrorthynchus* spp. (Table 2). All these records are new host and locality records.

### Family Centrorthynchidae

A single juvenile male, *Centrorthynchus* sp. 1, was found in *Herpetotheres cachinnans* (Linnaeus, 1758); Paraguay, Santa Sofia 10E, 11.10.1988 (INVE 38398). The measurements were as follows: Trunk 3 mm long, 435 at widest part, proboscis 600 long, 215 wide, neck 165 by 215, proboscis receptacle 871 by 188, the lemnisci tubular, extending posteriorly beyond the proboscis receptacle, 1220 long and the testes; anterior 82.5 by 56, posterior 89 by 19.5. The proboscis was armed with 26 rows of 24 hooks per row comprising 6 true hooks + 16 spiniform hooks.

A single juvenile female, also a centrorthynchid, (Figs 1-4) was found in *Turdus amaurochalinus* Cabanis, 1850; Paraguay, S-Lorenzo N 10E 16.10.1987 (MHNG-INV-82726). Since the anterior trunk of this specimen had 2 irregular rows of small spines although otherwise conforming to the diagnosis of the genus *Centrorthynchus* it could not be assigned to any known genus at this time. Measurements were: Trunk length 4.3 mm, maximum width 850; proboscis 617 long by 201 wide; neck 207 by

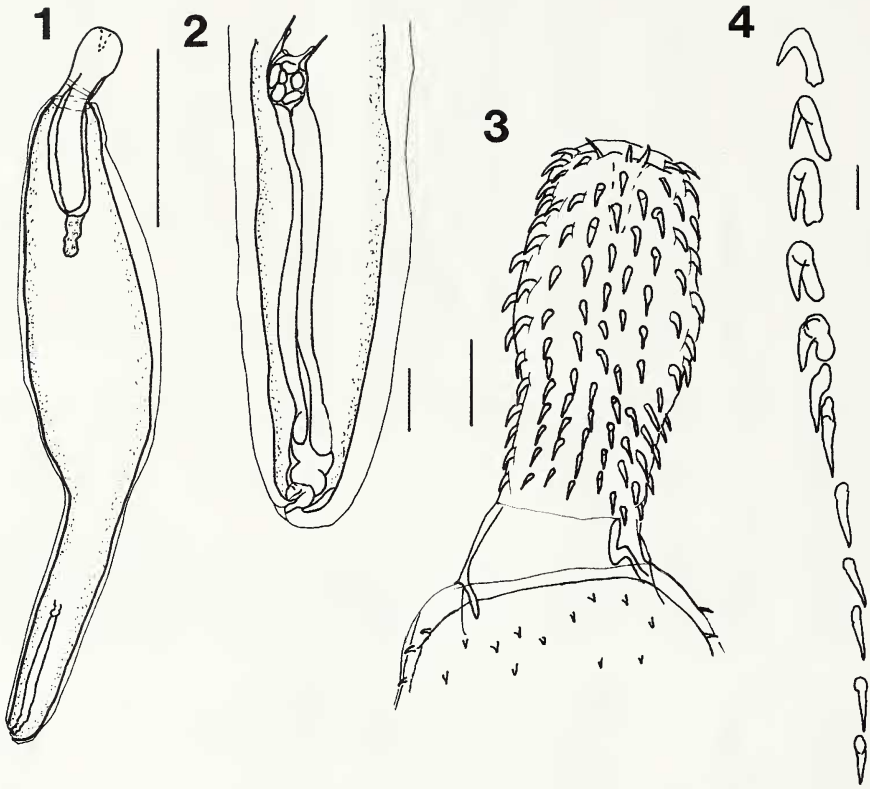
TABLE 1. Acanthocephala: Centrorhynchidae and Plagiorhynchidae from 21 bird hosts from Paraguay, South America collected between 1982 and 1989.

Host	Host field no. Py	Locality	Dept.	Geographical coordinates	Acanthocephalan
<b>Ciconiiformes: Ardeidae</b>					
<i>Ardea alba</i> Linnaeus, 1758	6609	Transchaco 180	Pte Hayes	-24.05 -58.37	<i>Lueheia inscripta</i> (Westrumb, 1821)
<b>Cuculiformes: Cuculidae</b>					
<i>Crotophaga ani</i> Linnaeus, 1758	2627	Santa Maria	Itapua	-26.99 -55.82	<i>Centrorhynchus guira</i> Lunaschi & Drago, 2010
<b>Falconiformes: Accipitridae</b>					
<i>Buteo magnirostris</i> (Gmelin, 1788)	2169	15 Km E from Cerrito	Paraguari	-26.39 -57.31	<i>Centrorhynchus varius</i> n. sp.
<b>Buteogallus meridionalis</b> (Latham, 1790)					
	6066	Puerto Militar 35	Pte Hayes	-23.52 -57.78	<i>Centrorhynchus varius</i>
	4079	Transchaco 110	Pte Hayes	-24.52 -58.03	<i>Centrorhynchus varius</i>
	4143	Pratts Gill	Boqueron	-22.56 -61.71	<i>Centrorhynchus varius</i>
	6682	Transchaco 293	Pte Hayes	-23.40 -58.99	<i>Centrorhynchus varius</i>
	4902	Transchaco 293	Pte Hayes	-23.40 -58.99	<i>Centrorhynchus varius</i>
<i>Buteogallus urubitinga</i> (Gmelin, 1788)	6589	Transchaco 70	Pte Hayes	-24.81 -57.77	<i>Centrorhynchus varius</i>
<i>Geranoaetus melanoleucus</i> (Vieillot, 1819)	6528	Aquidaban	Concepcion	-23.11 -57.62	<i>Centrorhynchus geranoaeti</i> n. sp.
<i>Parabuteo unicinatus</i> (Temminck, 1824)	6068	Transchaco 115	Pte Hayes	-24.48 -58.05	<i>Centrorhynchus varius</i>
<b>Falconidae</b>					
<i>Herpethores cachinnans</i> (Linnaeus, 1758)	7334	Santa Sofia 10E	Concepcion	-22.33 -57.07	<i>Centrorhynchus</i> sp.
<b>Passeriformes: Furnariidae</b>					
<i>Synallaxis</i> sp.	7250	S-Lorenzo N 10E	Central	-26.78 -57.49	<i>Lueheia inscripta</i>
<b>Turdidae</b>					
<i>Turdus amaurochalinus</i> Cabanis, 1850	7372	S-Lorenzo N 10E	Central	-26.78 -57.49	<i>Lueheia inscripta</i>
	7373	S-Lorenzo N 10E	Central	-26.78 -57.49	<i>Lueheia inscripta</i>
	7373	S-Lorenzo N 10E	Central	-26.78 -57.49	<i>Centrorhynchidae</i>
<b>Tyrannidae</b>					
<i>Pitangus sulphuratus</i> (Linnaeus, 1766)	3281	Arroyo Tagatiya-Guazu	Concepcion	-22.76 -57.45	<i>Centrorhynchus pitangi</i> n. sp.
<b>Thamnophillidae</b>					
<i>Taraba major</i> (Vieillot, 1816)	4891	Arroyo Agua-Pey	Itapua	-27.13 -56.28	<i>Centrorhynchus pitangi</i>
	4895	Arroyo Agua-Pey	Itapua	-27.13 -57.28	<i>Centrorhynchus pitangi</i>
<b>Strigiformes: Strigidae</b>					
<i>Megascops choliba</i> (Vieillot, 1817)	7360	S-Lorenzo N 10E	Central	-26.78 -57.49	<i>Lueheia inscripta</i>
	2123	Arroyo Agua-Pey	Itapua	-27.13 -56.28	<i>Centrorhynchus millerae</i> n.sp.
	4886	Arroyo Agua-Pey	Itapua	-27.13 -57.28	<i>Centrorhynchus millerae</i>



TABLE 2. Adults and cystacanths of Acanthocephala, collected from bird hosts in Paraguay, South America between 1982 and 1989, which could not be fully identified.

Host	Host field no. Py registration	Helminth no. INVE	Locality	Department	Geographical coordinates	Notes
<b>Caprimulgiformes:</b> Caprimulgidae <i>Caprimulgus parvulus</i> Gould, 1837	4748	38450	Rio Piribebuy	Cordillera	-25.08 -57.35	3 pieces of adult
<b>Cuculiformes:</b> Cuculidae <i>Guira guira</i> (Gmelin, 1788)	5363	38381	Itaipu	Alto Parana	-25.02 -54.50	cystacanth, proboscis inverted possibly <i>Centrorhynchus</i> sp.
<b>Passeriformes:</b> Dendrocolaptidae <i>Campylorhamphus trochilirostris</i> (Lichtenstein, 1820)	7417	38403	S Lorenzo N 10E	Central	-26.78 -54.49	cystacanth, <i>Centrorhynchus</i> sp.
<i>Lepidocolaptes angustirostris</i> (Vieillot, 1819)	2229	38473	Est. Montiel Potrero	Paraguari	-26.39 -57.31	1 cystacanth, probably <i>Centrorhynchus</i> sp.
<b>Emberizidae</b> <i>Emberizoides herbicola</i> (Vieillot, 1817)	3487	38438	Tobati	Cordillera	-25.28 -57.09	1 female, no proboscis or proboscis receptacle
<b>Hirundinidae</b> <i>Stelgidopteryx ruficollis</i> (Vieillot, 1817)	4273	38458	Rio Guazu, Rte 3	San Pedro Jejuí	-24.10 -56.45	1 female, no proboscis possibly <i>Mediorhynchus</i> sp.
<b>Icteridae</b> <i>Chrysomus cyanopus</i> (Vieillot, 1819)	8274	38140	General Diaz	Alto Paraguay	-21.13 -58.52	1 female, no proboscis or proboscis receptacle
<b>Thraupidae</b> <i>Oryzoborus angolensis</i> (Linnaeus, 1766)	6899	38396	Arroyo Tapiracuai	San Pedro	-24.60 -56.49	cystacanths, proboscis inverted
<b>Thamnophilidae</b> <i>Taraba major</i> (Vieillot, 1816)	4082	38436	Transchaco 293	Pte Hayes	-23.40 -58.99	cystacanths probably <i>Lueheta inscripta</i>
<b>Turdidae</b> <i>Turdus amaurochalinus</i> Cabanis, 1850	4813	48453	Pedro P Pena	Boqueron	-22.45 -62.35	no proboscis, probably <i>Lueheta inscripta</i>
<b>Tyrannidae</b> <i>Myiarchus tyrannulus</i> (Statius Muller, 1776)	3585	38435	Rte Montania	Boqueron Madrignon 20	-21.97 -59.95	2 females, no proboscis
<i>Tyrannus savana</i> Vieillot, 1808	4200	38441	Rio Guazu, Rte 3	San Pedro Jejuí	-24.10 -56.45	1 female juvenile, no proboscis
<b>Piciformes:</b> Dendrocolaptidae <i>Melanerpes cactorum</i> (d'Orbigny, 1840)	8813	38423	Pozo Arias	Pte Hayes	-23.65 -60.10	1 female no proboscis or proboscis receptacle
<b>Trogoniformes:</b> Trogonidae <i>Trogon curucui</i> Linnaeus, 1766	8071 8193	38408 38424	Puente Zinho Arroyo Tagatija-mi	Concepcion Concepcion	-22.38 -56.91 -22.69 -57.58	cystacanths, proboscis inverted 2 pieces of adult



FIGS 1-4

Centrorhynchid species. (1) Juvenile female. (2) Posterior end showing female reproductive tract. (3) Female proboscis showing armature. (4) Proboscis hooks, longitudinal row, hooks 3-14, showing true, transitional and spiniform hooks. Scale bars: 1, 1 mm; 2, 3, 100  $\mu$ m; 4, 25  $\mu$ m.

268, proboscis receptacle 1005 by 282; lemnisci tubular, longer than proboscis receptacle, 1020; reproductive tract 792 long, genital pore subterminal. The proboscis was armed with 20 or 22 rows of 14 hooks, 7 true hooks + 2 transitional hooks + 5 spiniform hooks; true and spiniform hooks with similar blade lengths, hooks 14 shortest in each row. Hook blade lengths in each longitudinal row: hooks 3, 39.6; 4, 33.0; 5, 33.0; 6, 42.9; 7, 42.9; 8, 39.6; 9, 39.6; 10, 42.9; 11, 46.2; 12, 39.6; 13, 36.3; 14, 29.7

The proboscis armatures of these two specimens differed from each other and from any of the species presently known from South America (Petrochenko, 1958; Lunaschi & Drago, 2010). The presence of spines on the anterior trunk of the female specimen does not fit the diagnosis of the genus *Centrorhynchus*, that is: trunk spineless, but does conform to the diagnosis in all other characters. More specimens are needed of both putative species of centrorhynchid however, before complete identifications and descriptions can be prepared.

***Centrorhynchus guira* Lunaschi & Drago, 2010**

Figs 5-12

MATERIAL EXAMINED: MHNG-INVE-38439; one male, pieces of a male and two females from *Crotophaga ani* Linnaeus, 1758, small intestine; Paraguay, Santa Maria, 28.10.1982.

COMMENTS: The proboscis armature of the specimens from *C. ani*, 32 longitudinal rows of 7-8 + 3-5 + 6-7, a total of 16-19 hooks per row, was consistent with that of *C. guira*. The armature of *C. guira* was described as 32 rows of 8-9 + 4 + 6, 18-19 hooks, although study of the photomicrograph, fig. 1b suggests that there are 5 transitional hooks in some rows (Lunaschi & Drago, 2010). The morphology and morphometrics of the specimens from *C. ani*, with the exception of the neck length, were also consistent with those of *C. guira* (see Table 3). The relevant photomicrograph, fig. 1a, given by Lunaschi & Drago (2010), is not clear although careful scrutiny suggests the neck length is more likely to be about 205-255, a measurement consistent with that of the specimens from *C. ani*, than the 30-68 given in the text. Examination of the male specimens in this study suggest that the genital pore is terminal as stated in Lunaschi & Drago (2010). In the photomicrograph fig. 1e (Lunaschi & Drago, 2010), however, the genital pore appears subterminal. In females the posterior end of the trunk is swollen and the genital pore is subterminal. Figures 5-12 are given here for *C. guira* to show the trunk shape and the relative proportions and positions of the internal organs because they were not illustrated in the original description.

The geographical range of *C. guira* has been extended from Argentina to Paraguay and the host range from *Guira guira* (Gmelin, 1788) to *Cryptopgaga ani*, both belonging to the cuckoo family, Cuculidae.

***Centrorhynchus geranoaeti* n. sp.**

Figs 13-19

MATERIAL EXAMINED: MNHG-INVE-82718; holotype, male, from the small intestine of *Geranoeatus melanoleucos* (Gmelin, 1788); Paraguay, Aquidaban, 12.10.1988. – MNHG-INVE-82719; paratype (allotype), female, from the small intestine of *Geranoeatus melanoleucos* (Gmelin, 1788); Paraguay, Aquidaban, 12.10.1988. – MNHG-INVE-38386; paratypes, male, 1 piece male, 2 females, 1 juvenile female, all from the small intestine of *Geranoeatus melanoleucos* (Gmelin, 1788); Paraguay, Aquidaban, 12.10.1988.

ETYMOLOGY: The species name is taken from the genus name of the host.

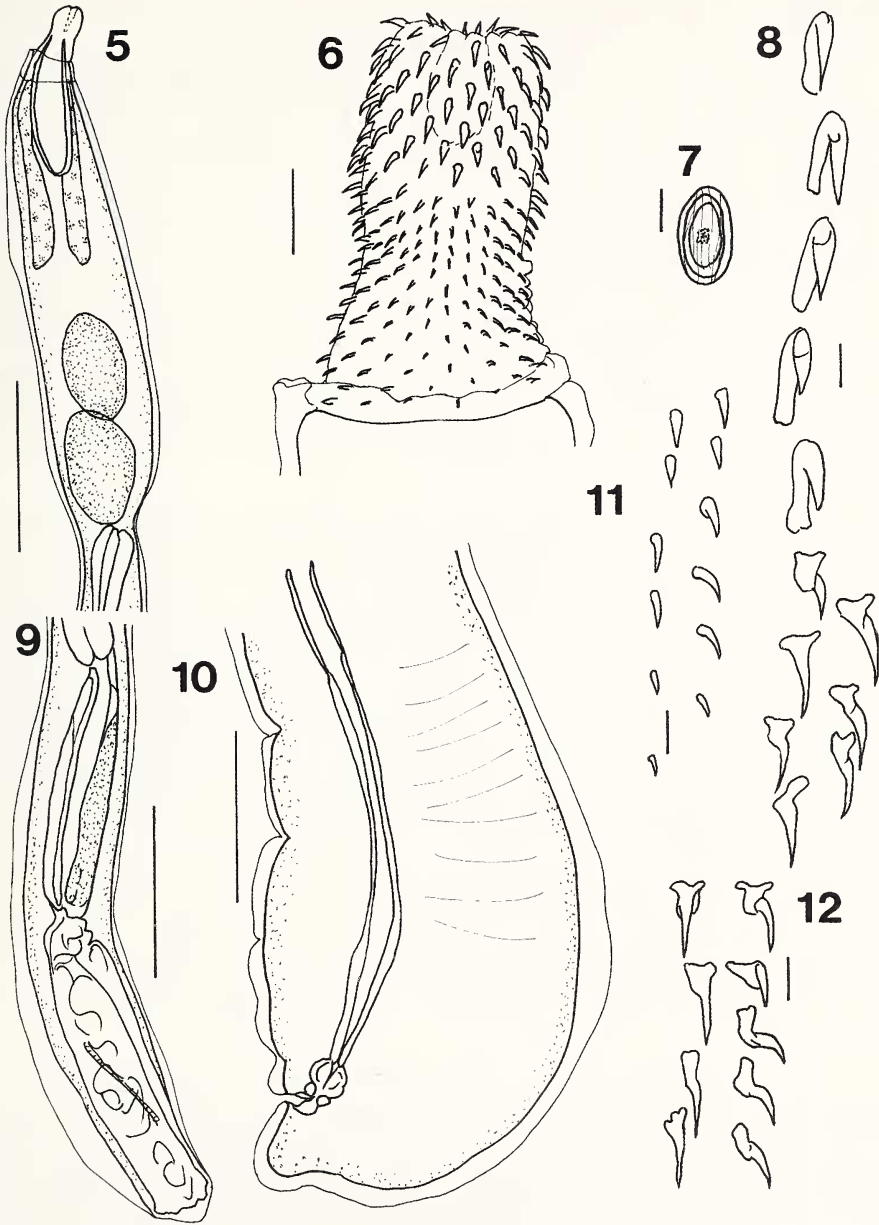
**DESCRIPTION**

General: (based on 2 males, 3 females, and 1 juvenile female) Trunk spineless, elongated; dilated anteriorly in region of testes in male, more or less cylindrical in female terminating in a digitiform process. Neck shorter than broad. Proboscis in 2 parts, slightly wider at base, with constriction anterior to insertion of proboscis receptacle, at about half way between apex and base of proboscis. Proboscis armature 30 rows 20-22 hooks, showing sexual dimorphism. Males: first 7-8 hooks in each longitudinal row with large simple roots, blades hooks 1-6/7 45-50 long, blades hooks 7/8 25 long; next 1-2 hooks with laterally extending shorter roots, blades 10-15 long; posterior 9-11 hooks spiniform, inserted on posterior part of proboscis, blades 10-20 long. Females: first 7-8 hooks with large simple roots, blades 1-7/8, 45-50 long, blades 7/8, 30 long; next 3-4 transitional hooks, blades 25 long; posterior 10-11 hooks spiniform, inserted on posterior part of proboscis, blades 10-30 long. Neck spineless, shorter than broad. Proboscis receptacle double walled. Lemnisci tubular, inserted at

TABLE 3. Comparative measurements of *Centrorhynchus albidus* and selected other species of *Centrorhynchus*, reported from South America, including species from this study; data from Travassos, 1926, Petrochenko, 1958, Schmidt & Neiland, 1966, Lunaschi & Drago, 2010.

	<i>C. albidus</i>	<i>C. geranoeti</i>	<i>C. giganteus</i>	<i>C. guira</i>	<i>C. millerae</i>	<i>C. pitangi</i>	<i>C. polymorphus</i>	<i>C. viarius</i>	<i>C. tumidulus</i>
				Argentina	Paraguay				
<b>Males</b>			young male						
Trunk length mm	12	15	12.5	26.1-30.9	30	13	6.5	12-18	15-24
Proboscis length	928-1250	1005	1870	790-970	805	650	670-880	804-1020	
Neck length	18	235		30-68	235-360	221		268-306	
width	372	636		410-510	470-510	370		382-510	
Proboscis receptacle length	1160-1250	1410		1400-1600	1200	1200	800-1000	1105-1785	1000-1160
Lemnisci length	1460-2500	1360	5200	1940-2340	2211	1250	1200-2000	1540	1300-2300
Anterior testis length	1000-568	502	300	1060-1200	1088	536	250	470-480	570
width	278	402	250	540-630	476-595	402	200	248-425	670
Posterior testis length		670		1110-1290	1139-1156	536		603-1190	
width		335	7.0	514-660	527-697	375		235-425	
Cement glands length mm		6.7			18.0-18.7	8.8	2.5-3.0	4.3-5.6	10.0-14.0
Saeffigen's pouch length		1400	1000	2710-2970	2380-3400	1300	1000	918-2210	1100-2300
<b>Females</b>			mature female						
Trunk length mm	16	21-22	37-55	38.8-50.4	50-55	25-35	9	12-35	15-37
Reproductive tract length		1206		2630	2145	900-2250		972-1340	
Proboscis length	1250	1105-1240		920-1000	805	850-900	804-1020	740-1072	
Proboscis receptacle length	1250	1530-1700		1690-1770	1700	1226-1810	1394-1615	1206-1581	
Lemnisci length	2500			1800-2710	2211	1445-1700	2200	1005-1335	
Egg length	42	49.5-56.0	56.0	53-64	46-53	49.5-56.0	44-50	42.5-49.5	53-56
width	20	23-29.5	28-32	24-29	23-30	23.0-29.5	22-30	18.5-23.0	21





FIGS 5-12

*Centrorhynchus guira* Lunaschi & Drago, 2010. (5) Male anterior end. (6) Male proboscis showing armature. (7) Egg. (8) Male proboscis hooks, showing part of longitudinal row of true hooks numbers 4, 5, 6, 7 and 8 and 2 rows of 3 transitional hooks numbers 9, 10, 11 and 9, 10, 11, 12 respectively. (9) Male posterior end. (10) Female posterior end showing bulbous shape and reproductive tract. (11) Male proboscis hooks showing longitudinal rows of 6 spiniform hooks. (12) Female proboscis, longitudinal rows of 4 and 5 transitional hooks showing manubria from differing orientations. Scale bars: 5, 9, 10, 1 mm; 6, 100  $\mu$ m; 7, 8, 11, 12, 25  $\mu$ m.

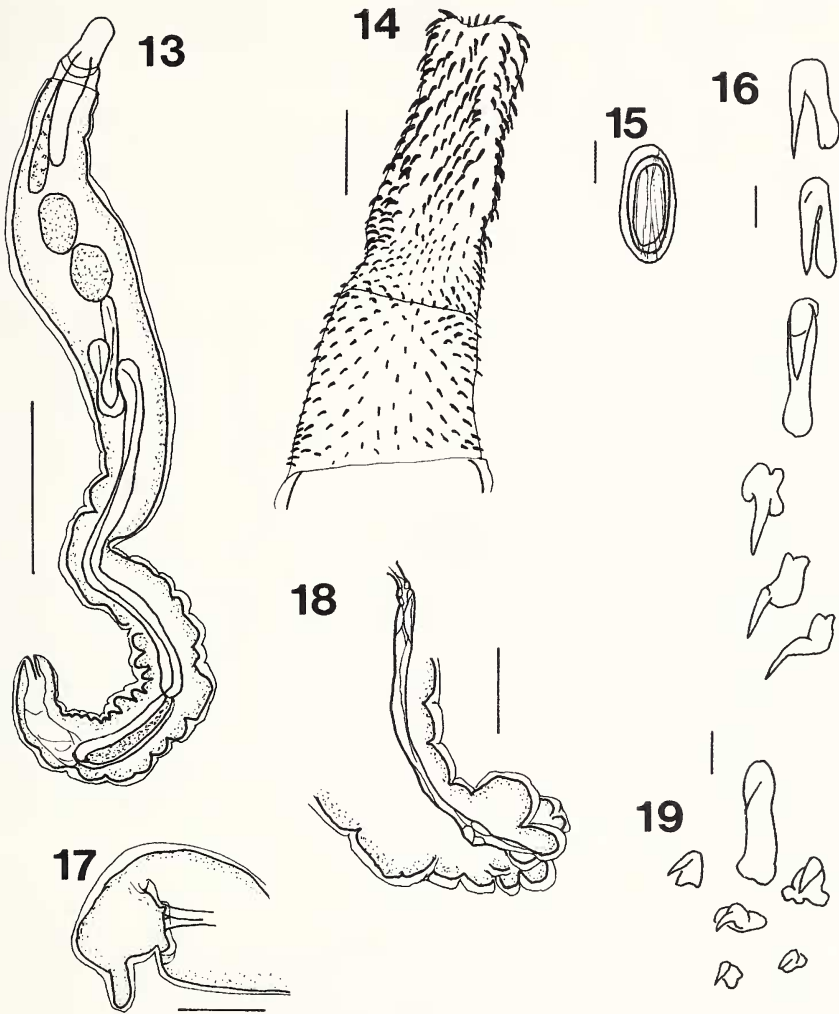
base of neck, extend posteriorly beyond proboscis receptacle. Cerebral ganglion located at mid region of proboscis receptacle, posterior to neck.

*Male:* (based on 2 specimens) Trunk 15 mm long, 1550 at widest part. Proboscis 1005 long, 335 wide. Neck 235 long, 635 wide at base. Proboscis receptacle 1410 long, 340 wide; lemnisci 1360 long. Testes oval, tandem, not contiguous, in anterior third of trunk; anterior testis 502 long, 402 wide; posterior testis 670 long, 335 wide. Cement glands, 3, elongated, tubular, begin immediately posterior to end of posterior testis, 6700 long; Saeftigen's pouch 1400 long. Genital pore terminal. Entire male system occupies about 88% trunk length.

*Female:* (Based on 3 specimens) Trunk 21, 22 mm long, 765, 940 wide. Proboscis 1105, 1240 long, 302, 425 wide. Neck 155, 235 long, 535, 605 wide at base. Proboscis receptacle 1530, 1700 long, 255, 325 wide. Lemnisci concealed by eggs. Reproductive tract, uterine bell to genital pore, 1206 long. Posterior end with digitiform papilla, genital pore subterminal. Eggs oval, external shell thick, ridged, 49.5-56.0 (52.8) long, 23.0-29.5 (25.6) wide.

COMMENTS: *Centrorhynchus geranoaeti* n. sp. conforms to the diagnosis of the genus given by Golvan (1956, 1960). *Centrorhynchus geranoaeti* differs from all other species of *Centrorhynchus* in that the female has typical transitional hooks with anteriorly extending manubria but the male does not. In males the anterior true hooks have large simple roots and the posterior ones short laterally extending roots. In the key to the Neotropical species of *Centrorhynchus* by Lunaschi & Drago (2010) *C. geranoaeti* with 30 longitudinal rows of 22-24 hooks, the transitionals with lateral alate processes, falls closest to *C. guira*, with 32 rows of 18-19 hooks, also with transitionals with lateral alate processes. *Centrorhynchus geranoaeti* can be further differentiated from *C. guira*, in having fewer, smaller, transitional hooks (2-3, 10-20 long, compared with 4-5, 19-33 long) and more spiniform hooks (9-11 compared with 6-7) in each longitudinal row. *Centrorhynchus geranoaeti* is a smaller worm than *C. guira*, with a longer proboscis, lemnisci not extending posteriorly beyond the proboscis receptacle, smaller testes, shorter cement glands, Saeftigen's pouch and female reproductive tract. The female trunk is more or less cylindrical, terminating in a digitiform process in *C. geranoaeti* and swollen posteriorly in *C. guira*. See Table 3 for comparative measurements.

*Centrorhynchus geranoaeti* with a proboscis armature of 30 rows of 22-24 hooks per row is also near to *C. albidus* and *C. polymorphus*, both having 28-30 rows of hooks and nearest to *C. albidus* that has 20-22 hooks per row (Schmidt & Neiland, 1966). Lunaschi & Drago (2010) interpret the proboscis armature of *C. albidus*, from figure 5 of Schmidt & Neiland (1966), as being up to 30 rows of 8 + 4 + 10 hooks per row. The descriptive text states "first 7 hooks in each row with well developed root, next hook with reduced root, next 13 or 14 hooks rootless" (Schmidt & Neiland, 1966). A careful study of figure 5, however, shows 8 hooks with true roots, the next with a reduced root and manubrium, then 3 with manubrium only and the last 10 rootless spines. Using this latter interpretation *C. geranoaeti* and *C. albidus* further differ in the number and form of each type of hook in each row (for males 8-10 hooks with large roots + 1-2 hooks with reduced roots + 9-10 spiniform hooks, compared with 7-8 hooks



FIGS 13-19

*Centrorhynchus geranoaeti* sp. n. (13) Male. (14) Female proboscis, showing armature. (15) Egg. (16) Female proboscis hooks, longitudinal row showing true hooks 8, 9, 10 and 3 transitional hooks. (17) Female posterior end. (18) Female posterior end showing reproductive tract, trunk contracted, posterior digitiform process inverted. (19) Male proboscis hooks, showing examples of a true hook with a large simple root and true hooks with reduced roots. Scale bars: 13, 1 mm; 14, 200  $\mu$ m; 15, 16, 19, 25  $\mu$ m; 17, 500  $\mu$ m; 18, 400  $\mu$ m.

with large roots + 1 hook with reduced root and manubrium + 3 transitional hooks + 9-11 spiniform hooks). *Centrorhynchus geranoaeti* has smaller testes and larger eggs than *C. albidus* (Table 3).

*Centrorhynchus geranoaeti* further differs from *C. polymorphus* in the number of hooks per row (22-24 compared with 17), body shape (cylindrical not claviform)

and length of proboscis, proboscis receptacle, cement glands and testis size (Table 3). Dimitrova & Gibson (2005) suggested that shape and size of the body and proboscis of *C. polymorphus* better fits the generic diagnosis of *Sphaerirostris* than of *Centrorhynchus* (see Golvan, 1956, 1960).

*Centrorhynchus simplex* Meyer, 1932, from Brazil was described only from juvenile forms encysted in the body cavity of a snake. The identity of the host is uncertain although the name given in the text, *Coluber olivaceus*, may be *Liophis poecilogyrus* (Wied-Neuwied, 1825). *Centrorhynchus simplex* can be distinguished from *C. geranoaeti* by the proboscis armature of 22-24 longitudinal rows of 24 hooks (Petrochenko, 1958).

Six species of *Centrorhynchus* are found in North America (Richardson & Nickol, 1995). *Centrorhynchus kuntzi* has also been recorded from Nicaragua and *C. microcephalus* from Mexico, both therefore being included in the key to the Neotropical species of *Centrorhynchus*. Of the remaining four species, *C. californicus* Millzner, 1924, *C. conspectus* Van Cleave & Pratt, 1940 and *C. robustus* Richardson & Nickol, 1995 have been reported only from the United States of America (Richardson & Nickol, 1995) and *C. spinosus* (Kaiser, 1893) from the United States and the Galapagos Islands (Van Cleave, 1924, 1940; Richardson & Nickol, 1995). *Centrorhynchus californicus*, *C. conspectus* and *C. robustus* can be distinguished from *C. geranoaeti* by their proboscis armature, having neither 30 longitudinal rows of hooks nor 10-12 true hooks, nor any transitional hooks in either male or female in each longitudinal row. *Centrorhynchus spinosus* is a larger worm than *C. geranoaeti* (male 30-45 mm compared with 15 mm), although with 32 rows of hooks it has a similar proboscis armature. However *C. spinosus* has no transitional hooks in either male or female and more spiniform hooks than *C. geranoaeti* (14-15 compared with 9-11) per row and the hooks of *C. spinosus* are larger than those of *C. geranoaeti* (48-60 compared with 10-50).

### *Centrorhynchus millerae* sp. n.

Figs 20-27

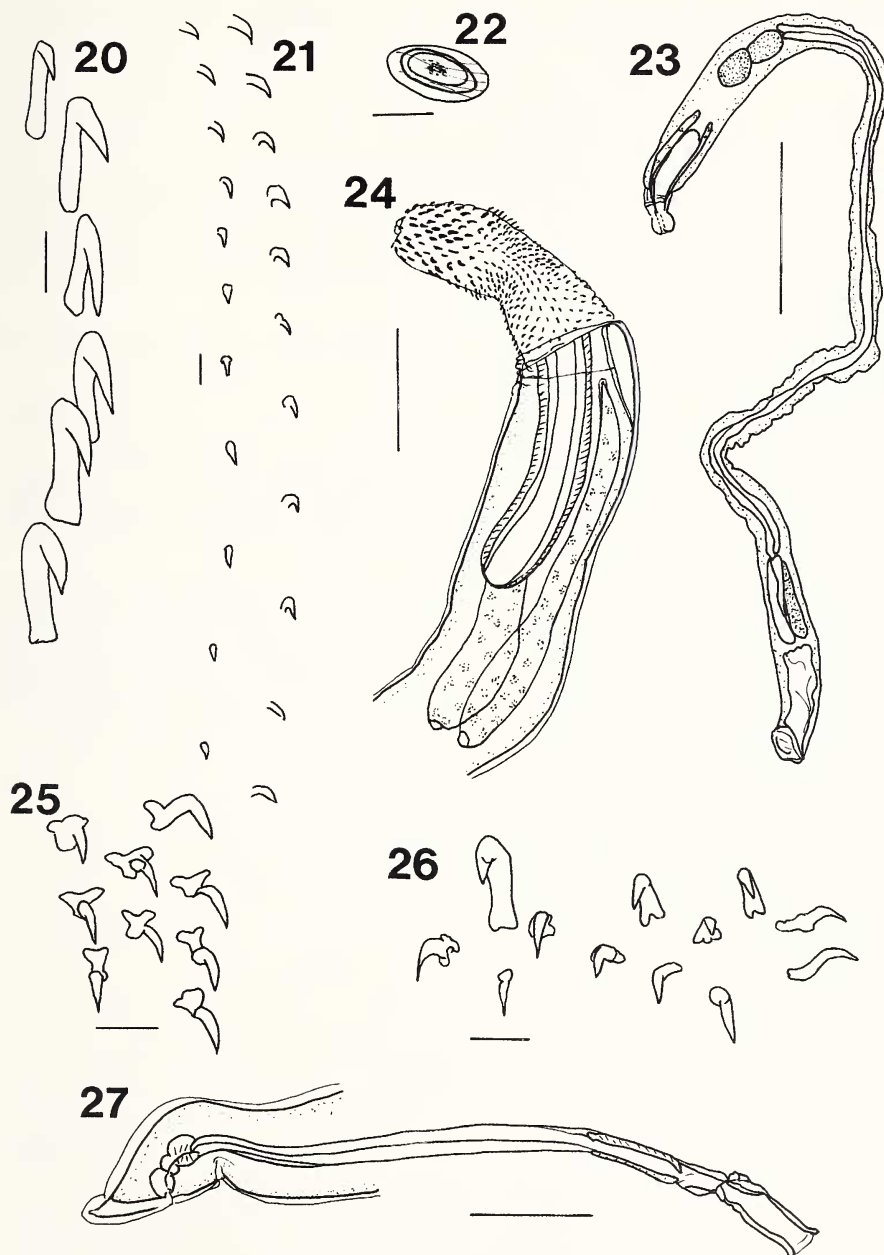
MATERIAL EXAMINED: MNHG-INVE-82720; holotype, male, from *Megascops choliba* (Vieillot, 1817), small intestine: Paraguay, Arroyo Agua-Pey, 25.10.1986. – MNHG-INVE-82721; paratype (allotype) female, from *Megascops choliba* (Vieillot, 1817), small intestine: Paraguay, Arroyo Agua-Pey, 25.10.1986. – MNHG-INVE-38444, paratypes 3 pieces female from *Megascops choliba* (Vieillot, 1817), small intestine: Paraguay, Arroyo Agua-Pey, 25.10.1986. – MNHG-INVE-38443; voucher specimens, 4 females, 6 pieces female from *M. choliba*, small intestine: Paraguay, Arroyo Agua-Pey, 10.10.1982.

ETYMOLOGY: This species is named in honour of the Director of the South Australian Museum.

### DESCRIPTION

*General:* (based on 1 male, 5 females, and 6 pieces of females) Trunk spineless, elongated; dilated anteriorly in region of testes in male, with swollen posterior end terminating in digitiform process in female. Neck shorter than broad. Proboscis in 2 parts, widest at base, with constriction at insertion of proboscis receptacle about 60% of distance from apex to proboscis base, anterior proboscis slightly expanded anterior to constriction. Proboscis armature 30-32 longitudinal rows 17-20 hooks, showing sexual





FIGS 20-27

*Centrorhynchus millerae* sp. n. (20) Female proboscis hooks, longitudinal row true hooks 1-6. (21) Female proboscis hooks, longitudinal row 11 spiniform hooks. (22) Egg. (23) Male. (24) Female, anterior end. (25) Female proboscis hooks, longitudinal rows 2-3 transitional hooks. (26) Male proboscis hooks, showing true hooks with simple roots and 1-2 hooks with reduced roots. (27) Female reproductive tract. Scale bars: 20, 22, 25, 26, 25 μm; 21, 12.5 μm; 23, 1 mm; 24, 27, 400 μm.

dimorphism. Male: in each longitudinal row first 5-6 hooks with large simple roots, blades 20-50 long, blades hooks 3, 45-50, longest, blades hooks 1, 6, 20-30, shortest; next hook with reduced root, blade 18-20 long, next 10-14 hooks spiniform, blades 11-15 long. Female: in each longitudinal row first 5-6 hooks with large simple roots, blades hooks 3 longest, blades hooks 1, 6 shortest; 3-4 transitional hooks with manubria, blades 20-25 long; next 9-12 hooks spiniform, blades 10-15 long, inserted on posterior part of proboscis. Neck spineless, shorter than broad. Proboscis receptacle double walled. Lemnisci elongated, claviform, inserted at base of neck, extend posteriorly beyond proboscis receptacle. Cerebral ganglion located at mid region of proboscis receptacle, posterior to neck.

*Male:* (based one specimen) Trunk 13 mm long, 1700 at widest part. Proboscis partly inverted estimated length 650, width 302. Neck 221 long, 370 wide at base. Proboscis receptacle 1200 long, 308 wide; lemnisci 1250 long. Testes oval, tandem, contiguous, in anterior third of trunk; anterior testis 536 long, 402 wide; posterior testis 536 long, 375 wide. Cement glands, 3 or 4 (number not determined), elongated, tubular, begin immediately posterior to end of posterior testis, 8800 long; Saeftigen's pouch 1300 long. Genital pore terminal. Entire male system occupies about 80% trunk length.

*Female:* (Based on 5 specimens) trunk 25-35 (29.5) mm long, 470-590 (575) wide. Proboscis 850-900 (875) long, 280-320 (299) wide. Neck 155-270 (203) long, 402-435 (420) wide at base. Proboscis receptacle 1226-1810 (1409) long, 205-340 (267) wide. Lemnisci 1445-1700 (1509) long. Reproductive tract, uterine bell to genital pore, 900-2250 (1575) long. Genital pore subterminal. Eggs oval, external shell thick, ridged, 49.5-56.0 (53.1) long, 23.0-29.5 (26.7) wide.

COMMENTS: *Centrorhynchus millerae* sp. n. conforms to the diagnosis of the genus given by Golvan (1956, 1960). *Centrorhynchus millerae* differs from all species of *Centrorhynchus*, except *C. geranoaeti*, in that only the females have a proboscis armature with transitional hooks. *Centrorhynchus millerae* differs from *C. geranoaeti* in the number hooks per row (16-20, of which 5-7 are true hooks compared with 22-24, 8-12) and the form of the transitional hooks, with lateral alate processes on the manubria for *C. millerae*, without for *C. geranoaeti*. *Centrorhynchus millerae* has a shorter proboscis and longer cement glands than *C. geranoaeti* (Table 3). *Centrorhynchus millerae* occurs in the passerine, *Pitangus sulfuratus*, the great kiskadee and *C. geranoaeti* in the strigiform, *Megascops cholida*, the tropical screech owl.

In the key to the Neotropical species of *Centrorhynchus* (Lunaschi & Drago, 2010) *C. millerae*, clusters together with *C. guira* and *C. kuntzi* as a third species with lateral alate processes on the transitional hooks. *Centrorhynchus millerae* is closest to, but differs from, *C. guira* in the number and arrangement of hooks of the proboscis armature (30-32 rows of 16-20 hooks compared with 32 rows of 16-19 hooks). *Centrorhynchus millerae* further differs from *C. guira* in having fewer true hooks and more spiniform hooks per row (5-6 and 9-14 compared with 7-9 and 6-7). *Centrorhynchus millerae* is a smaller worm than *C. guira* and has shorter lemnisci, smaller testes, shorter cement glands and shorter female reproductive tract (Table 3).

*Centrorhynchus simplex*, also from South America, and each of the species of *Centrorhynchus* from North America, as discussed above for *C. geranoaeti*, can be

further distinguished from *C. millerae* by their proboscis armature, having differing combinations of true and spiniform hooks and no transitional hooks.

***Centrorhynchus pitangi* n. sp.**

Figs 28-37

**MATERIAL EXAMINED:** MNHG-INVE-82722; holotype male from *Pitangus sulfuratus* (Linnaeus, 1776), small intestine: Paraguay, Arroyo Agua-Pey, 26.10.1986. – MNHG-INVE-82723; paratype (allotype) female from *Pitangus sulfuratus* (Linnaeus, 1776), small intestine: Paraguay, Arroyo Agua-Pey, 26.10.1986. – MNHG-INVE-38406; paratypes, from *Pitangus sulfuratus* (Linnaeus, 1776), small intestine: Paraguay, Arroyo Agua-Pey, 26.10.1986. – MNHG-INVE-38448; voucher specimens, 1 female, from *Pitangus sulfuratus* (Linnaeus, 1776), small intestine: Paraguay, Arroyo Agua-Pey, 26.10.1986. – MNHG-INVE-38447; 1 juvenile, from *P. sulfuratus* small intestine: Paraguay, Arroyo Tagatiya- Guiazu 17.10. 1983.

**ETYMOLOGY:** The species name is taken from the genus name of the host.

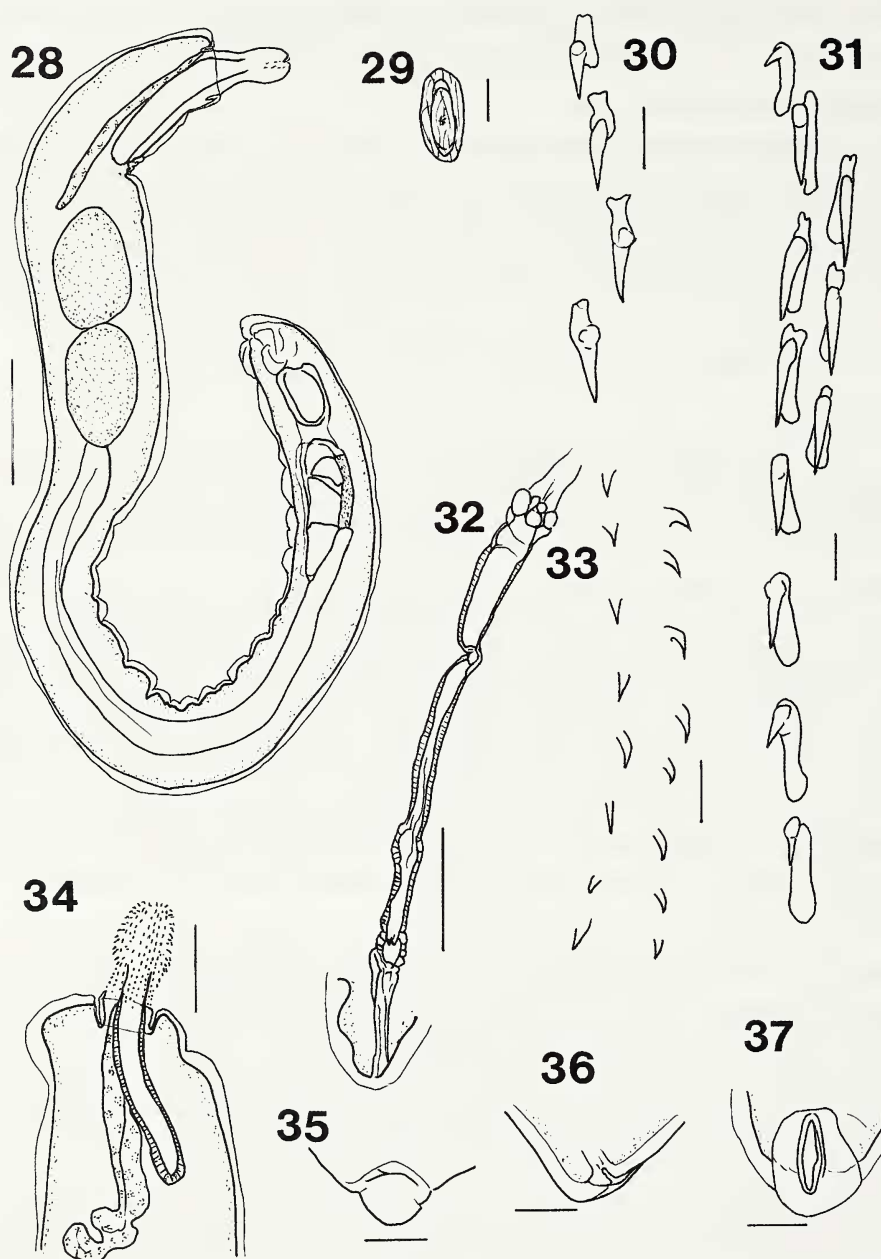
**DESCRIPTION**

*General:* (based on 2 males, pieces of 2 males, 5 females, and pieces of 5 females) Trunk spineless, elongated; more or less cylindrical in female, dilated anteriorly in region of testes in male. Neck shorter than broad. Proboscis in 2 parts, with constriction at insertion of proboscis receptacle, at about 62% of distance from apex to proboscis base, anterior proboscis slightly expanded above constriction. Proboscis armed with 28-30 longitudinal rows 18-20 hooks. Anterior 7-8 hooks with large simple roots, first 4 also with manubria, blades hooks 1, 13.2, 39.6 long, hooks 2, 46.2, 49.5 long, hooks 3, 42.9 long, hooks 4, 39.6, 42.9 long, hooks 5, 36.3-39.6 long, hooks 6, 33- 36.3 long, hooks 7, 33 long, hooks 8, 26.4, 29.7 long; next hook with reduced root and manubrium, blade 27 long; following 3 transitional hooks with manubria, blades 33-39.5 long; posterior 7-8 hooks spiniform, blades 10-30 long, inserted on posterior part of proboscis. Neck spineless, shorter than broad. Proboscis receptacle double walled. Lemnisci tubular, inserted at base of neck, extend posteriorly beyond proboscis receptacle. Cerebral ganglion located at mid region of proboscis receptacle, posterior to neck.

*Male:* (based on two specimens) Trunk 9, 11 mm long, 1360 at widest part. Proboscis 1005, 1020 long, 280, 301 wide. Neck 268, 402 long, 670, 735 wide at base. Proboscis receptacle 1360, 1307 long, 201-306 wide; lemnisci 2800 long. Testes oval, tandem, contiguous, in anterior third of trunk; anterior testis 1700, 1105 long, 476, 731 wide; posterior testis 1870, 1105 long, 510, 782 wide. Cement glands, 3, elongated, tubular, begin immediately posterior to end of posterior testis, 5100 long; Saeffigen's pouch 1200 long. Genital pore subterminal. Entire male system occupies about 85% trunk length.

*Female:* (Based on 5 specimens) Trunk 16-19 (18) mm long, 1190-1615 (1465) wide. Proboscis 804-1020 (946) long, 301-368 (320) wide. Neck 335-402 (370) long, 470-670 (570) wide at base. Proboscis receptacle 1394-1615 (1495) long, 238-295 (252) wide. Lemnisci 2200 long. Reproductive tract, uterine bell to genital pore, 2000 long. Genital pore subterminal. Eggs oval, external shell thick, ridged, 56.0-66.3 (58.8) long, 26.4-32.3 (27.9) wide.

**COMMENTS:** *Centrorhynchus pitangi* sp. n. conforms to the diagnosis of the genus given by Golvan (1956, 1960). In the key to the Neotropical species of



FIGS 28-37

*Centrorhynchus pitangi* sp. n. (28) Male. (29) Egg. (30) Proboscis hooks, longitudinal row 4 transitional hooks. (31) Proboscis hooks, longitudinal row true hooks 1-8, 4 with manubria. (32) Female genital tract, dissection. (33) Proboscis hooks, longitudinal rows 8 spiniform hooks. (34) Female anterior end. (35) Female posterior tip of trunk, ventral view. (36) Female posterior tip of trunk, lateral view. (37) Male posterior tip of trunk, bursa inverted, ventral view. Scale bars: 28, 32, 1 mm; 29, 30, 31, 33, 25  $\mu$ m; 34, 500  $\mu$ m; 35, 36, 37, 100  $\mu$ m.



*Centrorhynchus* by Lunaschi & Drago (2010) *C. pitangi* falls close to *C. giganteus* Travassos, 1926 in the form of the true hooks, both species having true hooks with manubria as well as transitional hooks with manubria. The two species differ in proboscis armature *C. pitangi* having 28-30 longitudinal rows of 18-20 hooks compared with 24-26 rows of 27-28 hooks for *C. giganteus*. Further the blades of the true hooks of *C. pitangi* are shorter than those of *C. giganteus* (13.5-43 compared with 100-150). Travassos (1926) does not use the term transitional hooks to describe hooks with manubria but no roots, separating the hooks only into 16-17 hooks and 11 spines in each row. His plate 9, figure 22, of hook types, however, shows at least one spine in each row was a transitional type, with manubrium and without a root. Therefore in comparing numbers of hook types in this instance, transitional hooks should be counted as true hooks. Accordingly *C. pitangi* would have 11-12 hooks and 7-8 spines compared with 16-17 hooks and 7-8 spines for *C. giganteus*. *Centrorhynchus pitangi* can be further distinguished from *C. giganteus* as a smaller worm (females 16-19 compared with 37-55mm long) with a shorter proboscis (up to 1020 long, compared with 1870), shorter lemnisci (2200-2800 compared with 5200 long) and smaller testes (up to 1870 compared with 3000 long) (Travassos, 1926).

Although not recognized by Lunaschi & Drago (2010) *C. tumidulus*, as described and figured by Travassos (1926, see p. 68 and fig. 5) also has true hooks with manubria. *Centrorhynchus pitangi* can be distinguished from *C. tumidulus* by the number of hooks of the proboscis armature (28-30 rows of 18-20 hooks compared with 26 rows of 20-21 hooks) and in having transitional hooks which *C. tumidulus* lacks. Further *C. pitangi* is a smaller worm with larger testes, longer lemnisci, shorter cement glands and larger eggs than *C. tumidulus* (Table 3).

*Centrorhynchus albidus* and *C. polymorphus* are the other species from South America having a proboscis armature of up to 30 longitudinal rows of hooks (Lunaschi & Drago, 2010). *Centrorhynchus pitangi* differs from both species in form of the true hooks. *Centrorhynchus pitangi* further differs from *C. albidus* in the total number of hooks per row (18-20 compared with 20-22 hooks) and the numbers of each type of hook, as interpreted above (7-8 true hooks, 4 with manubria + 1-2 true hooks with reduced root and manubrium + 2-3 transitional hooks + 7-8 spiniform hooks compared with 7-8 true hooks + 1 hook with reduced root and manubrium + 3 transitional hooks + 10-11 spiniform hooks) (Schmidt & Neiland, 1966). *Centrorhynchus pitangi* has larger testes and larger eggs than *C. albidus* (Table 3).

*Centrorhynchus pitangi* further differs from *C. polymorphus* in proboscis armature, the total number of hooks per row (18-20 compared with 17) and the number of each type of hook in each row (8-9 including true hooks with manubria + 2-3 + 7-8 compared with 7+3+7) (Travassos, 1926), as well as in body length and shape, cylindrical not claviform, the length of the proboscis, proboscis receptacle, cement glands and Saeftigen's pouch and the size of the testes and eggs (Table 3).

*Centrorhynchus pitangi* differs from all other species found in Paraguay, *C. guira*, *C. geranoaeti* and *C. millerae* in proboscis armature, both in the morphology and the numbers of true hooks and spines. *Centrorhynchus guira* has 32 rows of 18-19 hooks, 4 being transitional hooks with lateral alate processes and 6 spiniform hooks. *Centrorhynchus geranoaeti* and *C. millerae* have females with and males without

transitional hooks in 30, 30-32 rows of 22-24 and 16-20 hooks including 9-11 and 9-14 spiniform hooks respectively.

*Centrorhynchus pitangi* can be distinguished from *C. opimus* by the number of longitudinal rows of proboscis hooks (28-30 compared with 24) and by having true hooks 8-9 with reduced roots and manubria. Travassos (fig. 27, plate 11, 1926) shows anterior true hooks with manubria and transitional hooks but not hooks with reduced roots and manubria. *Centrorhynchus pitangi* has a shorter trunk (9-11 compared with 12-16 for males) longer lemnisci (2200-2800 compared with 2000) and longer cement glands (5100 compared with 2700) than *C. opimus*.

*Centrorhynchus simplex*, found in Brazil, can be distinguished from *C. pitangi* by the proboscis armature. Similarly *C. pitangi* can be differentiated from each of the four species of *Centrorhynchus* found only in North America by a combination of the characters of the proboscis armature; numbers, arrangement, morphology and sizes of hooks as detailed for *C. geranoaeti* above.

### *Centrorhynchus viarius* n. sp.

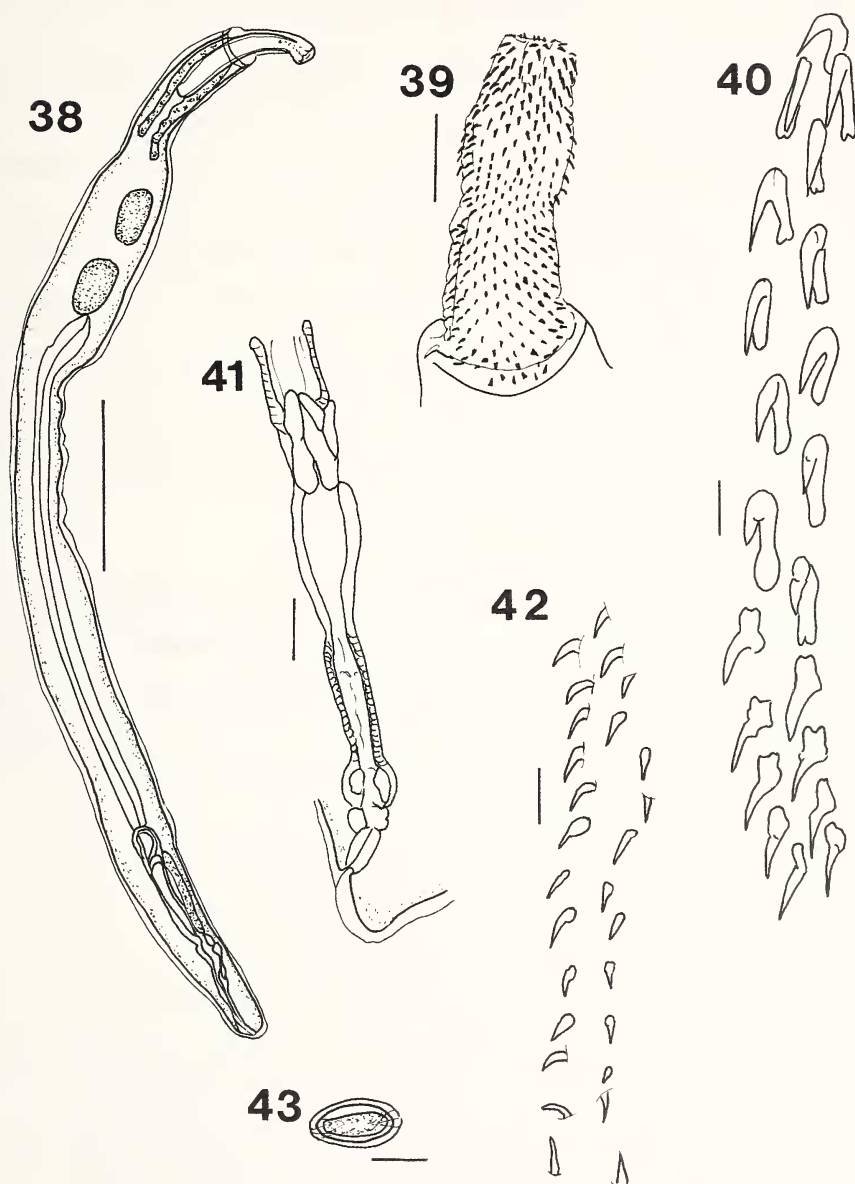
Figs 38-43

MATERIAL EXAMINED: MHNG-INVE-82724; holotype, male, from *Buteogallus meridionalis* (Latham, 1790), small intestine; Paraguay, Transchaco 293, Pte Hayes; 04.11.1983. – MHNG-INVE-82725, paratype (allotype), female, from *Buteogallus meridionalis* (Latham, 1790), small intestine; Paraguay, Transchaco 293, Pte Hayes; 04.11.1983. – MHNG-INVE-38393; paratypes from *Buteogallus meridionalis* (Latham, 1790), small intestine; Paraguay, Transchaco 293, Pte Hayes; 04.11.1983. – MHNG-INVE-38455, voucher specimens, 1 female, from *Buteogallus meridionalis* (Latham, 1790), small intestine; Paraguay, Transchaco 293, Pte Hayes; 05.07.1985. – MNHG-INVE-38459, 38456, 38457, 383843, juvenile males, pieces of males, 5 females, pieces of females from *Buteo magnirostris* (Gmelin, 1788), small intestine; Paraguay, Transchaco 95, 110, 15 km E from Cerrito, Pratts Gill, 12.10.1982, 01.08.1951995, 01. 07.1995, 07.11.1987. – MHNG-INVE-38388, 1 female from *Buteogallus urubitinga* (Gmelin, 1788), small intestine; Paraguay, Transchaco 70, 24.10.1988. – MNHG-INVE-38385, 1 male, 5 pieces female from *Parabuteo uncinatus* (Temminck, 1824), small intestine; Paraguay, Transchaco 115, 07.11.1987.

ETYMOLOGY: The species name is taken from *viari*, of the roadside, and refers to the fact that all the hosts were collected from along the Transchaco.

### DESCRIPTION

*General*: (based on 5 males, 3 juvenile males, 14 pieces of male, 12 females and 35 pieces of female) Trunk spineless, elongated, more or less cylindrical, dilated anteriorly in region of testes. Neck shorter than broad. Proboscis in 2 parts, with constriction at insertion of proboscis receptacle at about 50% of distance from apex to proboscis base; anterior proboscis slightly expanded above constriction. Proboscis armed with 28-30 rows 23-27 hooks, lengths of hook blades vary irregularly along each row, longest blades usually hooks 3-5, shortest blades, usually hooks 19-22. Anterior 8-9 hooks with large simple roots, blades hooks 2, 35 long, hooks 3, 32, 38 long, hooks 4, 38, 40 long, hooks 5, 20-40 long, hooks 6, 35-40 long, hooks 7, 30-40 long, hooks 8, 20-32 long, hooks 9, 25 long; next 4-5 hooks transitional, blades 18-30 long; posterior 12-13 hooks spiniform, inserted on posterior part of proboscis, longest blades last 2 hooks in row, 10-30 long. Neck spineless, shorter than broad. Proboscis receptacle double walled. Lemnisci tubular, inserted at base of neck, extend posteriorly



FIGS 38-43

*Centrorhynchus viarius* sp. n. (38) Male. (39) Male proboscis, showing armature. (40) Proboscis hooks, longitudinal rows of true hooks 3-7, 2-8, and transitional hooks 5, 4. (41) Female reproductive tract. (42) Proboscis hooks, longitudinal rows of spiniform hooks 13, 14. (43) Egg. Scale bars: 38, 1 mm; 39, 200  $\mu$ m; 40, 42, 43 25  $\mu$ m; 41, 100  $\mu$ m.

beyond proboscis receptacle. Cerebral ganglion located at mid region of proboscis receptacle, posterior to neck.

*Male:* (Based on 5 specimens) Trunk 12-18 (14) mm long, 490-835 (693) wide. Proboscis 805-1020 (871) long, 268-306 (298) wide. Neck 268-340 (315) long, 382-510 (470) wide at base. Proboscis receptacle 1105-1785 (1334) long, 181-290 (220) wide; lemnisci (single measurement) 1540 long. Testes oval, tandem, not contiguous, in anterior third of trunk; anterior testis 470-840 (727) long, 248-425 (296) wide; posterior testis 603-1190 (828) long, 235-425 (344) wide. Cement glands, 4, elongated, tubular, begin immediately posterior to end of posterior testis, 4335-5610 (4972) long; Saeftigen's pouch 918-2210 (1309) long. Genital pore terminal. Entire male system occupies about 85-90% of trunk length.

*Female:* (Based on 7 specimens) trunk 12-35 (19) mm long, 510-1020 (755) wide. Proboscis 740-1072 (871) long, 268-335 (306) wide. Neck 201-536 (358) long, 402-570 (486) wide at base. Proboscis receptacle 1206-1581 (1407) long, 227-325 (267) wide. Reproductive tract, uterine bell to genital pore, 972-1340 (1184). Genital pore subterminal. Eggs oval, external shell thick, ridged, 42.5-49.5 (46.0) long, 18.5-23.0 (21.5) wide.

COMMENTS: *Centrorhynchus viarius* sp. n. conforms to the diagnosis of the genus given by Golvan (1956, 1960). In the key to the Neotropical species of *Centrorhynchus* of Lunaschi & Drago (2010) *C. viarius* falls within the group of species with a proboscis armature which has transitional hooks without lateral alate processes, namely *C. albidus*, *C. polymorphus*, *C. crotophagicola* and *C. microcephalus*. With a proboscis armature of 28-30 rows of 23-27 hooks *C. viarius* clusters with *C. albidus* and *C. polymorphus* each of which has up to 30 rows of hooks (Lunaschi & Drago, 2010).

In terms of number of hooks per row *C. viarius* is closest to *C. albidus*, but differs in the number and type of hooks per row (8-9+4-5+12-13 compared with 7-8+3-4+10). The hooks of *C. viarius*, are smaller and more variable in size, 18-40 for hooks with roots and 10-30 for spiniform hooks, compared with 44 for hooks on the first third of the proboscis and 35 elsewhere for *C. albidus* (Schmidt & Neiland, 1966). None of the specimens of *C. viarius* examined in this study had hooks with reduced roots and manubria as figured by Schmidt & Neiland (1966). *Centrorhynchus viarius* further differs from *C. albidus* in the number of cement glands (4, as determined by transverse section, for *C. viarius*, 3 for *C. albidus*) (Schmidt & Neiland, 1966). Both species occur in Falconidae from Paraguay but *C. viarius* has been found in hawks, *Buteo magnirostris*, *Buteogallus meridionalis*, *B. urubitinga* and *Parabuteo uncinctus* while *C. albidus* has been reported from the plumbeous kite *Ictinia plumbea* (Gmelin, 1788) (see Golvan, 1956).

Of the species of *Centrorhynchus* also found in Paraguay *C. viarius* with a proboscis armature of 28-30 longitudinal rows of hooks is closest to *C. pitangi*, also with 28-30 rows of hooks. *Centrorhynchus viarius* differs from *C. pitangi* in the number of hooks per row (23-27 compared with 18-20) the form of the true hooks (all without manubria compared to hooks 1-4 with manubria and large simple roots and hooks 7-8 with manubria and reduced roots) as well as the number of spiniform hooks



(7-8 compared to 12-13). *Centrorhynchus viarius* is a longer worm than *C. pitangi* and has shorter lemnisci, smaller testes and smaller eggs (Table 3). *Centrorhynchus viarius* can be differentiated from *C. guira*, a larger worm, in the number of hooks per row (23-27 compared with 18-19), the form of the manubria of the transitional hooks and the number of spiniform hooks (6 compared with 12-13). *Centrorhynchus viarius* can be differentiated from *C. opimus* by the number of rows of proboscis hooks (24 compared with 28-30) and the form of the true hooks (all without manubria compared to some with manubria). *Centrorhynchus viarius* further differs from *C. geranoeti* and *C. millerae* in the number of hooks per row (23-27 compared with 22-24 and 16-20 respectively) and the form of the true hooks (males and females having all true hooks with large simple hooks and transitional hooks compared with males having some true hooks with reduced hooks and no transitional hooks) and from *C. simplex* in the number of rows and hooks per row. Comparative measurements are given in Table 3. *Centrorhynchus viarius* differs from *C. simplex* in proboscis armature (28-30 longitudinal rows of 23-27 hooks compared with 22-24 longitudinal rows of 22-24 hooks).

Of the four species of *Centrorhynchus* known only from North America *C. spinosus*, with 30-32 longitudinal rows of 23-28 hooks, has a similar proboscis armature to that of *C. viarius*. *Centrorhynchus spinosus*, a much larger worm (females up to 60 mm long), can be differentiated from *C. viarius* by having 8-9 true hooks, no transitional hooks and 13-15 spiniform hooks in each row. The females of *C. spinosus* have two genital papillae.

KEY TO THE NEOTROPICAL SPECIES OF *CENTRORHYNCHUS*; based on Lunaschi & Drago (2010).

- 1a Proboscis armature of 22-24 longitudinal rows of 24 hooks per row;  
14 true hooks + 10 spines . . . . . *C. simplex* Meyer, 1932
- 1b Proboscis armature not as above . . . . . 2
- 2a Proboscis armature with manubria on some true hooks . . . . . 3
- 2b Proboscis armature without manubria on true hooks . . . . . 6
- 3a Proboscis armature without transitional hooks . *C. tumidulus* (Rudolphi, 1819)
- 3b Proboscis armature with transitional hooks . . . . . 4
- 4a Proboscis armature of 28-30 longitudinal rows of 18-20 hooks per row;  
8-9+2+7-8 . . . . . *C. pitangi* sp. n.
- 4b Proboscis armature of less than 28 longitudinal rows of hooks . . . . . 5
- 5a Proboscis armature of 24-28 longitudinal rows of 27-28 hooks per row;  
16-17+1+10-11 . . . . . *C. giganteus* Travassos, 1921
- 5b Proboscis armature of 24 longitudinal rows of 12-13 hooks; 8-9 true +  
transitional hooks + 3-4 spines . . . . . *C. opimus* Travassos, 1921
- 6a Proboscis armature with transitional hooks in female only . . . . . 7
- 6b Proboscis armature with transitional hooks in both male and female . . . . . 8
- 7a Proboscis armature with 30-32 longitudinal rows of 16-20 hooks per  
row; male 6-7+9-14, female 5-6+3-4+10 transitionals with lateral pro-  
cesses . . . . . *C. millerae* sp. n.
- 7b Proboscis armature with 30 longitudinal rows of 22-24 hooks per row;  
male 11-12+9-10, female 8-10+3-4+9-10 transitionals without lateral  
processes . . . . . *C. geranoeti* sp. n.

- 8a Proboscis armature with transitional hooks with lateral processes . . . . . 9
- 8b Proboscis armature with transitional hooks without lateral processes . . . . . 10
- 9a Proboscis armature with 26-35 longitudinal rows of 22-27 hooks per row; 7-9+2+14-18 . . . . . *C. kuntzi* Schmidt & Neiland, 1966
- 9b Proboscis armature with 30-32 longitudinal rows of 18-19 hooks per row; 8-9+4+6 . . . . . *C. guira* Lunaschi & Drago, 2010
- 10a Proboscis armature of more than 30 longitudinal rows of hooks . . . . . 11
- 10b Proboscis armature of up to 30 longitudinal rows of hooks . . . . . 12
- 11a Proboscis armature of 32-35 longitudinal rows of 15-17 hooks per row; 8-9+3+4-5 . . . . . *C. crotophagicola* Schmidt & Neiland, 1966
- 11b Proboscis armature of 36-38 longitudinal rows of 17-18 rows of hooks; 9+3+5 . . . . . *C. microcephalus* Bravo Hollis, 1947
- 12a Proboscis armature of 28-30 longitudinal rows of 20-22 hooks; 8+4+10 . . . . . *C. albidus* Meyer, 1932
- 12b Proboscis armature of 28-30 longitudinal rows of 23-27 hooks; 8-9+4-5+12-13 . . . . . *C. viarius* sp. n.

## Family Plagiorhynchidae

### *Lueheia inscripta* (Westrumb, 1821)

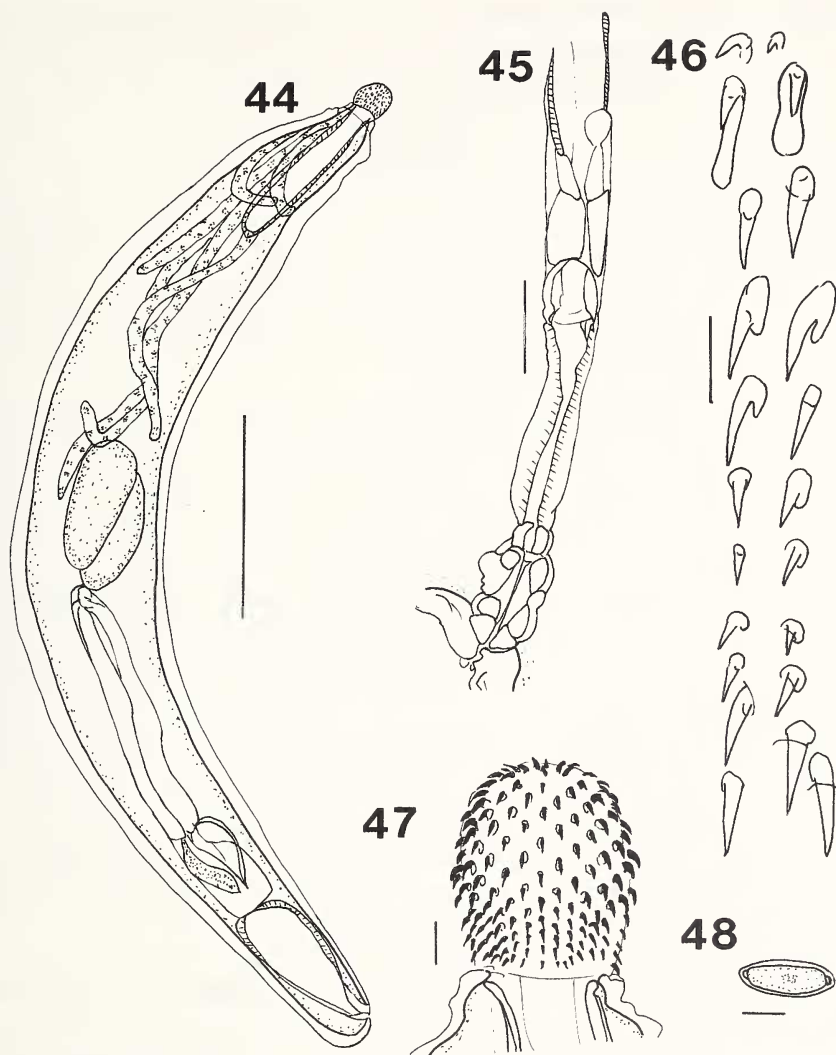
Figs 44 - 48

MATERIAL EXAMINED: MHNG-INVE-38401, MNHG-INVE-38402; voucher specimens, 2 males, 5 females, 20 juveniles, from small intestine, *Turdus amaurochalinus* Cabanis, 1850; Paraguay, S. Lorenzo N 10 E, 16.10.1987, 16.10.1989. – MHNG-INVE-48453; voucher specimen, 1 male, from small intestine, *T. amaurochalinus*; Paraguay, Pedro P Pena, 8.10.1986. – MHNG-INVE-38389; voucher specimens, 2 females, from small intestine, *Ardea alba* Linnaeus, 1758; Paraguay, Transchaco 180, 28.10.1988. – MHNG-INVE-38436; voucher specimens, 3 juveniles, from small intestine *Taraba major* (Vieillot, 1816); Paraguay, Transchaco 293, 04.07.1985. – MHNG-INVE-38400; 15 immature specimens, proboscides inverted, from small intestine, *T. major*; Paraguay, S. Lorenzo 10 E, 16.10.1989. – MHNG-INVE-38399. 1 female, *Synallaxis* sp. S. Lorenzo N 10 E, 16.10.1989.

### REDESCRIPTION

*General*: [Based on 3 males, 4 females, 40 immature or juvenile specimens and Travassos (1926)]. Trunk spineless, elongated, fusiform. Proboscis subglobular to semispherical; armed with 28-30 rows 9-12 hooks; largest hooks located mid proboscis, first and last 2 hooks in row 17-25 long, other hooks 40-56 long. Neck spineless, short, longer than wide in female. Proboscis receptacle double walled. Lemnisci 2, each subdivided into 3 long slender parts of varying lengths inserted at base of neck, extend posteriorly reaching beyond anterior testis. Cerebral ganglion located at mid region of proboscis receptacle.

*Male*: Trunk 8-11 (9.5) mm long, 1200-1530 (1365) wide. Proboscis 380-600 (480) long, 310-430 (400) wide. Neck 348 long, 348 wide at base. Proboscis receptacle 1375-1615 (1530) long, 320-340 (330) wide; lemnisci (single measurement) longest parts 4760, shortest parts 2550. Testes oval, contiguous, in middle third of trunk; anterior testis 1000-1205 (1135) long, 400-630 (522) wide; posterior testis 1000-1200 (1075) long, 375-500 (460) wide. Cement glands, 4, (by dissection) elongated, tubular, begin immediately posterior to end of posterior testis, 1900-2550 (2385) long. Genital pore subterminal. Entire male system occupies about 65% of trunk length.



FIGS 44-48

*Lueheia inscripta* (Westrumb, 1821) (44) Male. (45) Female reproductive tract. (46) Proboscis hooks, longitudinal rows of 11 hooks. (47) Female proboscis, showing armature. (48) Egg. Scale bars: 44, 1 mm; 45, 150 µm; 46, 48, 25 µm; 47, 100 µm.

*Female*: Trunk 7-15 (10.4) mm long, 1870-2200 (1990) wide. Proboscis 425-530 (477) long, 402-420 (410) wide just anterior to constriction. Hook lengths 2 longitudinal rows 25, 23; 42, 40; 50, 49; 49, 50; 45, 49; 45, 40; 40, 40; 40, 40; 50, 40; 35, 25; 30, 25. Neck 201 long, 445 wide at base. Proboscis receptacle 1570-1700 (1637) long, 300-325 (312) wide. Reproductive tract, uterine bell to genital pore, 1070-1140 (1105). Genital pore subterminal. Eggs oval, external shell thick, with polar protrusions of the fertilization membrane, 59.5-78.0 (63.0) long, 23.0-28.0 (24.0) wide.

COMMENTS: Although identified as early as 1821 (Westrumb) and redescribed by Travassos (1926) from specimens occurring in Turdidae from Brazil, the descriptions of *L. inscripta* were brief and gave only limited morphometric data, especially for females. More recently Whittaker *et al.* (1970b) reported *L. inscripta* from grackles, *Quiscalis niger* (Boddaert, 1783) and Acholonu (1976) reported juvenile males and females from lizards *Anolis cristatellus* Duméril & Bibron, 1837 from Puerto Rico. Subsequently Salgado-Maldonado & Caspeta-Mandujano (2010) reported on juveniles in frogs, *Lepidodactylus fragilis* Brochi, 1877 and a toad *Bufo marinus* (Linnaeus, 1758). These latter authors provided comprehensive descriptions of both male and female juveniles and demonstrated that the morphology and morphometrics of their specimens from paratenic hosts were congruent with those of adult specimens of *L. inscripta* from passerine birds (Table 4).

Although *L. inscripta* and *L. adlueheia* have been considered synonyms by some authors (see for example Schmidt & Neiland, 1966), they should now both accepted as valid species, on the basis of reexamination of specimens and reevaluation of characters (Van Cleave & Williams, 1952; Salgado-Maldonado & Caspeta-Mandujano, 2010). Both *L. inscripta* and *L. adlueheia* have similar proboscis armature (28-30 longitudinal rows of 9-12 hooks compared with 28 rows of 9-10 hooks) and hook size (largest blades 63 compared with 62 long) but they can be distinguished by a suite of other characters. *Lueheia inscripta* differs from *L. adlueheia* in having a larger proboscis, shorter cement glands, longer Saeftigen's pouch, larger eggs and the number of branches of the lemnisci and their lengths (4-6 of varying lengths compared with 6-10 of similar lengths) (Table 4).

*Lueheia inscripta* differs from the type species *L. lueheia* in proboscis armature (28-30 rows of 9-12 hooks compared with 20-22 rows of 8-9 hooks). Both species have 6 lemnisci but those of *L. inscripta* are of varying lengths while those of *L. lueheia* are of similar lengths. The testes of *L. inscripta* are larger (1000-1205 long compared with 700) and the eggs smaller (59.5-78 by 23-28 compared with 78-80 by 28-31) (Travassos 1921, 1926).

The proboscis armature of *L. cajabambensis* is not described except to say that the form and number of hooks differs from those of *L. lueheia* and *L. inscripta*. *Lueheia inscripta* further differs from *L. cajabambensis* in having up to 6 lemnisci compared with only 4, smaller testes (1000-1205 compared with 1748-1992 long), shorter cement glands (1900-2550 compared with 4834) and shorter Saeftigen's pouch (600-700 compared with 1909) (Machado-Filho & Nicanor-Ibáñez, 1967).

A new species, *L. karachiensis*, was described from 3 males occurring in *A. b. cenchroides* from Karachi, Pakistan. As described, the only character suggesting that these specimens are of the genus *Lueheia* is the presence of 4 lemnisci. The body shape of this species both from the description and figure appears more like *Centrorhynchus* than *Lueheia* as does the placement of testes in anterior third of the trunk and the proportions of the reproductive system. The description of the proboscis, subglobular with no measurements given, differs from the more or less cylindrical shape depicted in the figure. The roots of the proboscis hooks are neither described nor drawn (Aly Khan *et al.*, 2005). Given that the other four species of *Lueheia* are found in passerine birds from the Americas and this species in a raptor from the Indian subcontinent it seems most



TABLE 4. Comparative information for *Lueheia inscripta* (Wertheim, 1821) and *L. adlueheia* (Werby, 1938). \*This measurement may be in error.

	<i>L. inscripta</i>	<i>L. inscripta</i> juveniles	<i>L. inscripta</i>	<i>L. adlueheia</i>
Reference	Travassos, 1926	Salgado-Maldonado & Caspeta- Mandujano, 1910	this study	Werby, 1938
<b>Male</b>				
Trunk length mm	8	2.4-3.6	8-11	3.5-9.2
Proboscis length	520-620	420-560	380-600	385-490
width	410-430	330-380	310-430	280-385
Neck length		190-270	348	126-210
width		270-330	348	
Proboscis receptacle length	1600	732-1108	1375-1615	749-1190
width	340	297-346	320-340	
Lemnisci, number	4-6	6	6	6-10
length		891-1336	2250-4760	840-1820
Anterior testis length	1000	270-366	1000-1205	231-1274
width	400-500	75-200	400-630	120-177
Posterior testis length		237-375	1000-1200	280-1267
width		62-265	375-500	154-776
Cement glands	1900	740-1087	1900-2550	700-3430
Saeffigen's pouch		28-43*	600-700	200-400
<b>Female</b>				
Trunk length mm	9-15	4.0-4.7	7-15	11.3-15
Proboscis length		540-610	425-530	399-602
width		370-410	402-420	315-525
Reproductive tract length	1900	800-1100	1070-1140	
Egg length	63-78		59.5-78	36-41
width	28		23-28	12.7-15.5
Hosts	Turdidae	Anura	Turdidae	Turdidae
Locality	Brazil	Mexico	Paraguay	Washington USA

likely that *L. karachiensis* should be re assigned, possibly to the genus *Centrorhynchus*. Multiple lemnisci have been recorded as anomalies in *Fillicollis sphaerocephalis* (Bremser in Rudolphi, 1819) now *Profillicollis sphaerocephalis*, *Pomphorhynchus proteus* now a synonym of *P. laevis* (Mueller, 1776) and *Plagiorhynchus formosus* now a synonym of *P. cylindraceus* (Goeze, 1782) (see Van Cleave, 1942) and could perhaps be the case in this instance. Until the identity of this species is resolved it should be relegated to incertae sedis.

DISCUSSION

Consistent characters for recognizing and defining acanthocephalans include the dimensions and morphology of the proboscis and its armature (Richardson & Nickol, 1995). For species of *Centrorhynchus* in particular, the number of longitudinal rows of hooks, number of hooks per row, size of blades and morphology and size of roots have great taxonomic value (Golvan, 1960). The morphology of the hooks: true (simple roots with or without manubria), transitional (reduced roots with manubria, with or without lateral alate processes) and spiniform (reduced roots without manubria), is consistently reliable and was used by Lunaschi & Drago (2010) in their key to Neotropical species of *Centrorhynchus*. An analysis of hook morphology suggests that the South American fauna can be grouped into species having some true hooks with manubria, *C. giganteus*, *C. opimus*, *C. pitangi*, and *C. tumidulus* and species having all



true hooks without manubria, *C. albidus*, *C. crotophagicola*, *C. geranoaeti*, *C. guira*, *C. kuntzi*, *C. microcephalus*, *C. millerae*, *C. nicaraguensis*, *C. pitangi*, *C. polymorphus*, *C. viarius*. Alternatively all, with the exception of *C. tumidulus*, found in Brazil, Columbia, Uruguay and Venezuela in South America and Panama in Central America, fall into a single group with transitional hooks. Additional evidence is needed however before potential relationships between these species can be determined.

The species occurring in Paraguay fall into two groups, those with lateral alate processes on the transitional hooks (*C. geranoaeti*, *C. guira*, and *C. millerae*) and those without (*C. albidus*, *C. pitangi* and *C. viarius*). Within the former group *C. geranoaeti* and *C. millerae* share the character of sexual dimorphism of the proboscis armature as well as that of the form of the transitional hooks suggesting a possible relationship between them and *C. guira* and *C. kuntzi* the only other species with lateral alate processes. *Centrorhynchus guira* is found in Argentina and Paraguay, *C. kuntzi* in The Galapagos, Nicaragua, Central America and Florida, United States of America. Each of the species in the latter group has a proboscis armature of 28-30 longitudinal rows of hooks. *Centrorhynchus pitangi* can also be linked with *C. giganteus*, *C. opimus* and *C. tumidulus* in having some true hooks with manubria. *Centrorhynchus giganteus* and *C. tumidulus* are also known from Panama, Central America and *C. opimus* only from Brazil. *Centrorhynchus albidus* and *C. viarius* share the characters of number of longitudinal rows of hooks and true hooks without manubria.

*Centrorhynchus opimus* Travassos, 1921 was originally described from the great kiskadee, *Pitangus sulfuratus* (Passeriformes: Tyrannidae), from Brazil and subsequently transferred to *Sphaerirostris* by Golvan (1956, 1960) because of the morphology of the hooks and its occurrence in passerine bird hosts. It has since been reported from Brazil, as *C. opimus* from the boat billed flycatcher, *Megarhynchus pitangua* (Linnaeus, 1766) (Vicente *et al.*, 1983) and was returned to *Centrorhynchus*, without discussion, by Golvan (1994). Lunaschi & Drago (2010) however did not include *C. opimus* in their key. A comparison of the generic diagnoses of *Centrorhynchus*, parasites of diurnal and nocturnal birds of prey and *Sphaerirostris*, parasites of the passerine families Turdidae, Corvidae and related families, to the descriptions of *C. opimus* by Travassos (1921, 1926) suggests that the cylindrical shape of the body and the elongated shape of the proboscis, as figured by Travassos (figs 25, 26, plate 10 and 27, plate 11, 1926) and Vicente *et al.* (fig. 10, 1983), are typical of *Centrorhynchus* spp. and not *Sphaerirostris* spp. Richardson & Nickol (1995) emphasized the importance of trunk shape as a useful characteristic. Golvan (1960) suggested that true hooks with manubria, as described for *C. opimus*, were seen only in the proboscis armature of species of *Sphaerirostris* but both *C. giganteus* occurring in Falconidae from Brazil and *C. pitangi* (this study) have true hooks with manubria (Travassos, 1926; Lunaschi & Drago, 2010). Hence true hooks, with and without manubria, are found in both genera. Moreover a species of *Centrorhynchus*, from Mexico *C. microcephalus* has been described from the passerine family Icteridae (see Richardson & Nickol, 1995), broadening the host range of some species of *Centrorhynchus* to selected passerine families. Therefore, since the shape and size of the body and proboscis of *C. opimus* better fits *Centrorhynchus* than *Sphaerirostris* and similarly shaped hooks are found in both genera, the placement of *C. opimus* is justified.

The taxonomic position of *C. polymorphus* has been previously suggested as equivocal (Dimitrova & Gibson, 1995; Lunaschi & Drago, 2010). Given the shape and size of the body and the proboscis these authors were of the opinion that *C. polymorphus* better fit *Sphaeroirostris* than *Centrorhynchus*. This is the same logic as was applied to the placement of *C. opimus* and is supported here. Therefore the Centrorhynchidae now known to occur in South America include 13 species of *Centrorhynchus*: *C. albidus*, *C. crottophagicola*, *C. geranoaeti*, *C. giganteus*, *C. guira*, *C. kuntzi*, *C. microcephalus*, *C. millerae*, *C. nicaraguensis*, *C. opimus*, *C. pitangi*, *C. tumidulus*, *C. viarius* as well as one species yet to be fully described and a species of *Sphaeroirostris*; *S. polymorphus*.

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